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EARLY TERTIARY OF UTAH AND COLORADO

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Vol. 76, No. 2, February, 1989
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ATTACHED REPRODUCTIVE AND VEGETATIVE REMAINS OF THE EXTINCT AMERICAN-EUROPEAN GENUS CEDRELOSPERMUM (ULMACEAE) FROM THE EARLY TERTIARY OF UTAH AND COLORADO¹

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ABSTRACT

Fossil twigs with attached foliage, fruits, and flowers from the middle Eocene of the Green River Formation in northeastern Utah and northwestern Colorado and from the early Oligocene Florissant beds of central Colorado provide a firm basis for reconstructing two species of an extinct ulmaceous genus that was widely distributed in the Tertiary of midlatitude western North America and Europe. The fruits are samaras of *Cedrelospermum* Saporta, a genus previously known only from isolated specimens. The distichously arranged, slender, pinnate-veined leaves vary from serrate with simple teeth to, less commonly, entire-margined. Corresponding isolated leaves in the Green River, Florissant, and other Eocene to Oligocene localities of western North America are now excluded from *Zelkova* and *Myrica*, to which they were previously misidentified. The anthers of the staminate flowers contain 3-5 porate pollen with rugulate sculpture. Based upon combined characters of phyllotaxy, and leaf, flower, fruit, and pollen morphology, *Cedrelospermum* can be referred to the extant subfamily Ulmoideae, and is similar to *Phyllostylon*, *Zelkova*, and *Hemiptelea*. The abundance of *Cedrelospermum* in lake sediments of volcanic areas, together with its production of numerous small winged fruits, suggest that it was an early successional colonizer of open habitats.

THE FOSSIL RECORD of the Ulmaceae, like that of most angiosperm families, is known mostly from isolated organs because of the tendency for leaves and other plant structures to be shed separately into the sedimentary environment. In the absence of physical attachment it is impossible to prove absolutely that a given leaf and fruit represent the same fossil species. Therefore, fossil twigs showing actual attachment between leaves and reproductive structures are important in providing the best possible basis for multiple organ reconstructions of extinct fossil species. Such reconstructions facilitate an unusually complete understanding of the plant's biology and systematic relationships.

Fossil twigs with mutually attached leaves

and reproductive structures are in general very rare; however, recovery of such specimens is more common in some taxonomic groups than in others. The dicotyledonous families Fagaceae (Smiley and Huggins, 1981; Manchester and Crane, 1983), Salicaceae (Manchester, Dilcher, and Tidwell, 1986), and Ulmaceae are each represented in Tertiary sediments by occasional specimens showing such connections. The phenomenon of "self-pruning," which has been reported in extant *Populus* and *Ulmus* (Broadhurst, 1917), may improve the probability of preserving whole twigs as fossils. In *Ulmus americana*, for example, mature branches are easily shed by snapping off cleanly at the annual rings or scars formed by the terminal bud scales (Broadhurst, 1917). Extant *Zelkova* frequently sheds branches with fruits and leaves still attached (Kirchheimer, 1957, and personal observation) and this may explain the recovery of numerous fossil twigs of *Zelkova zelkovifolia* (Ung.) Bůžek and Kotlaba with attached fruits and leaves from the Tertiary of Europe (e.g., Kovats, 1856, pl. 6, fig. 2-5; Saporta, 1891, pl. 19, fig. 4, 8; Manchester, in press, fig. 5A-C), and Asia (Kutuzkina, 1982; Ishida, 1970, pl. 10, fig. 5, 6; Hu and Chaney, 1940, pl. 16, fig. 3; Manchester, in press, fig. 5D).

This paper considers the extinct ulmaceous genus *Cedrelospermum* Saporta in a whole-

Received for publication 22 February 1988; revision accepted 21 June 1988.

Important specimens were contributed by Ed and Ava Le, William Crepet, Bruce Handley, Dennis Kingery, Jack Wolfe, and were observed in museum and university collections through the courtesy of the curators indicated in the materials and methods. Helpful comments and discussion were provided by R. J. Burnham, P. R. Crane, P. Grote, H. Jähnichen, D. L. Dilcher, D. H. Mai, R. R. Rüttele, B. H. Tiffney, and J. A. Wolfe. Figure 48 was prepared by Meredith Morse. This investigation was aided by NSF grants BSR 84-07841 and EAR 87-07523 to the author, and by NSF facilities grant PCM 82-12660 to the Indiana University Biology Department for the purchase and maintenance of SEM equipment.

species and genus (Unger, 1850) is clearly distinct from the later-assigned material and is not ulmaceous (Manchester, 1987). The North American fruits were formerly assigned to *Banksites* (Lesquereux, 1883; Cockerell, 1925; Brown, 1940) and *Lomatia* (MacGinitie, 1953, 1969) and, together with some co-occurring leaf impressions, were regarded as "clear proof of the presence of Proteaceae in the flora" (MacGinitie, 1953, p. 109). With the discovery of specimens showing the fruits attached to twigs bearing an unexpected kind of foliage, they were removed from the Proteaceae (MacGinitie, 1974, p. 68). Detailed morphological study of the isolated American and European fruits (Manchester, 1987) and of the other parts of the plant considered in the present paper provide the basis for recognition of *Cedrelospermum* as an extinct genus of Ulmaceae.

In North America, leaves corresponding to *Cedrelospermum* have been assigned to a variety of extant genera, including *Myrica*, *Salix*, and perhaps most convincingly, *Zelkova* (Brown, 1946; MacGinitie, 1953, 1969, 1974; Burnham, 1986). Tanai and Wolfe (1977, p. 1) were the first to indicate that this leaf type might represent an extinct ulmaceous genus, based on their preliminary examination of a branchlet of such leaves with attached flowers (Fig. 15), and excluded it from their revision of fossil *Ulmus* and *Zelkova* foliage from western North America. Based upon analyses of numerous isolated leaves, Burnham (1986) interpreted the fossils to represent extant *Zelkova*, but she considered them to represent a distinct morphotype ("Morphotype B"). These fossil leaves are indeed similar to those of *Zelkova*, but are typically distinguished by narrower laminae and less prominent marginal teeth, as well as various fruit and floral differences presented herein.

The completeness with which *Cedrelospermum* can be reconstructed enables consideration of the relationship of this genus to others in the Ulmaceae. Functional morphology and stratigraphic and geographic distribution provide insight into the ecology and history of this extinct genus.

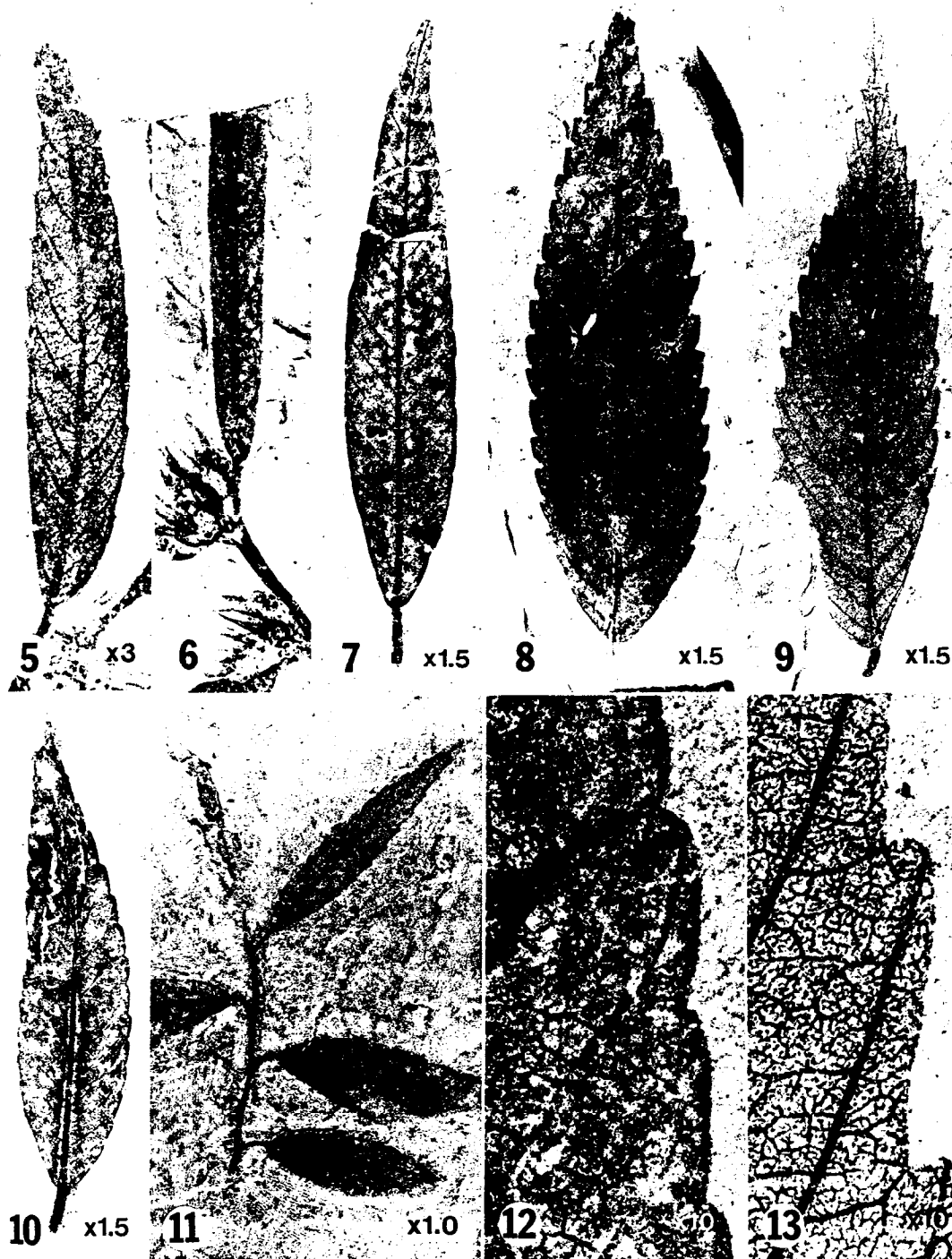
MATERIALS AND METHODS—Critical specimens showing the linkage between leaves and

reproductive structures were located by surveying large collections from the Green River Formation and Florissant beds, notably those of the United States National Museum, Washington, DC (USNM; courtesy J. P. Ferrigno, S. L. Wing), the Peabody Museum, Yale University, New Haven, Connecticut (YPM; courtesy L. J. Hickey, B. H. Tiffney), the Geological Survey, Denver, Colorado (USGS; courtesy J. A. Wolfe), Indiana University (IU; courtesy D. L. Dilcher) and private collectors Bruce Handley, Dennis Kingery, and Ed and Ava Cole. Specimens contributed by private collectors and those collected through fieldwork of the author were catalogued into the IU collection. The descriptions presented in this paper incorporate data from isolated fruits and foliage, as well as from attached specimens, to give a more complete perspective of the range of variation in these organs. Isolated fruits and leaves from the Green River and Florissant beds were studied and measured at the Museum of Paleontology, University of California, Berkeley (UCMP; courtesy H. Schorn), the Field Museum of Natural History, Chicago (FM; courtesy P. Crane), University of Colorado Museum, Boulder (UCM; courtesy P. Robinson), the Denver Natural History Museum, Colorado (DNHM; courtesy P. Jablonski), and at Michigan State University, East Lansing (MSU; courtesy R. Taggart, A. T. Cross), Department of Geology, Waynesburg College, Waynesburg, Pennsylvania (WC; courtesy R. Carnein) as well as at the institutions listed above.

The Green River specimens cited here are all from the Parachute Creek member of the Green River Formation, which is well known for its fossil flora (MacGinitie, 1969). Although the localities extend from northeastern Utah to northwestern Colorado, they represent the same lacustrine sequence and this member is considered to be middle Eocene (Grande, 1984). The Florissant specimens are from lacustrine shales near Florissant in central Colorado. The Florissant beds are well known for their diverse fossil flora (MacGinitie, 1953) and are lower Oligocene based on a radiometric date of about 35 million years (m.y.; Epis and Chapin, 1974; corrected to new constant) and acceptance of 37 m.y. as the Eocene-Oligocene boundary.

While material from the Green River and

Fig. 5–13. Leaves of *Cedrelospermum nervosum* from the Green River Formation, Utah and Wyoming. Fig. 5–13. 5. Leaf with prominent teeth along the margin and craspedodromous venation from a twig with attached fruits; counterpart of specimen in Fig. 4. $\times 3$. 6. Entire-margined, nearly symmetrical leaf with camptodromous venation, from a twig with attached fruits; detail from specimen in Fig. 1. $\times 3$. Fig. 7–10. Isolated larger leaves, probably of



vegetative twigs, showing variability in length/width ratios, symmetry and margin. 7. Lanceolate, nearly symmetrical leaf with margin grading from entire near the base to faintly crenulate toward the apex, Watson, Utah, IU 15885-7349. $\times 1.5$. 8. Lectotype (Orig. Newberry, 1898, pl. 67, fig. 2), nearly symmetrical leaf with prominent, blunt, simple teeth and stout midvein, USNM 7307, Green River, Wyoming. $\times 1.5$. 9. Leaf with asymmetrical lamina and prominent teeth, Watson, Utah, IU 15883-7351. $\times 1.5$. 10. Elliptical, nearly symmetrical leaf with obtuse teeth, Watson, Utah, IU 15755-7352. $\times 1.5$. 11. Vegetative twig with elliptical to lanceolate leaves and small rounded axillary buds. Note that the leaves are larger than those on the fruiting and flowering twigs. Watson, Utah, IU 15884-7308. $\times 1$. 12. Detail from Fig. 10, showing submedial, concave, entry of secondary veins into teeth, well developed tertiary and higher order venation. $\times 10$. 13. Margin of a leaf with prominent sharp to rounded teeth and excellently preserved venation. Note the strong tertiary veins vascularizing the tooth sinuses, and the branched freely ending veinlets, Watson, Utah, IU 15754-7353. $\times 10$.

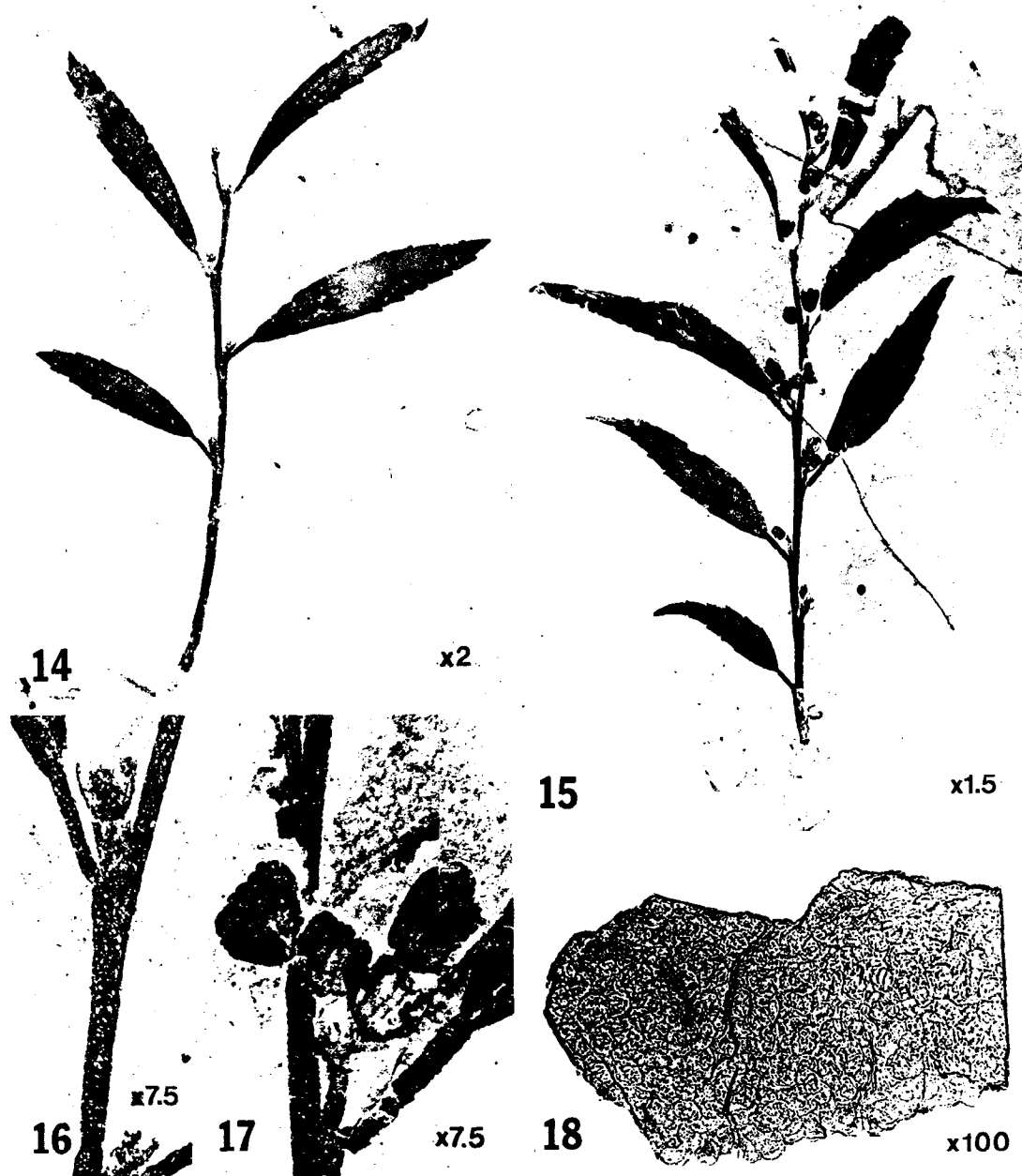


Fig. 14-18. Flowering twigs of *Cedrelospermum nervosum* from the middle Eocene Green River Formation, Utah and Colorado. 14. Specimen with probable pistillate flowers in the leaf axils, Watson, Utah, IU 15751-7042. $\times 2$. 15. Specimen with staminate flowers, USGS loc. 8642, Carr Creek, Colorado. USNM 414096. $\times 1.5$. 16. Detail of flowers from Fig. 14, showing two pedicels and three incipient fruit wings. $\times 7.5$. 17. Detail of axillary staminate flowers from Fig. 15, showing groups of stamens in each flower, composite photo prepared from negatives of both counterparts. $\times 7.5$. 18. Mass of pollen removed from stamen of Fig. 17. $\times 100$.

Florissant beds is important in authenticating the multiple-organ reconstruction provided here, specimens from other parts of North America and Europe are important in understanding the distribution and variability of species in this extinct genus. Specimens from the Eocene Clarno Formation of Oregon were

studied in the collections of the Oregon Museum of Science and Industry (OMSI) and IU. Isolated fruits and foliage from the Oligocene Catahoula Formation of Texas were provided from the University of Connecticut (courtesy W. L. Crepet) and University of Texas (courtesy T. Delevoryas). Specimens from the upper

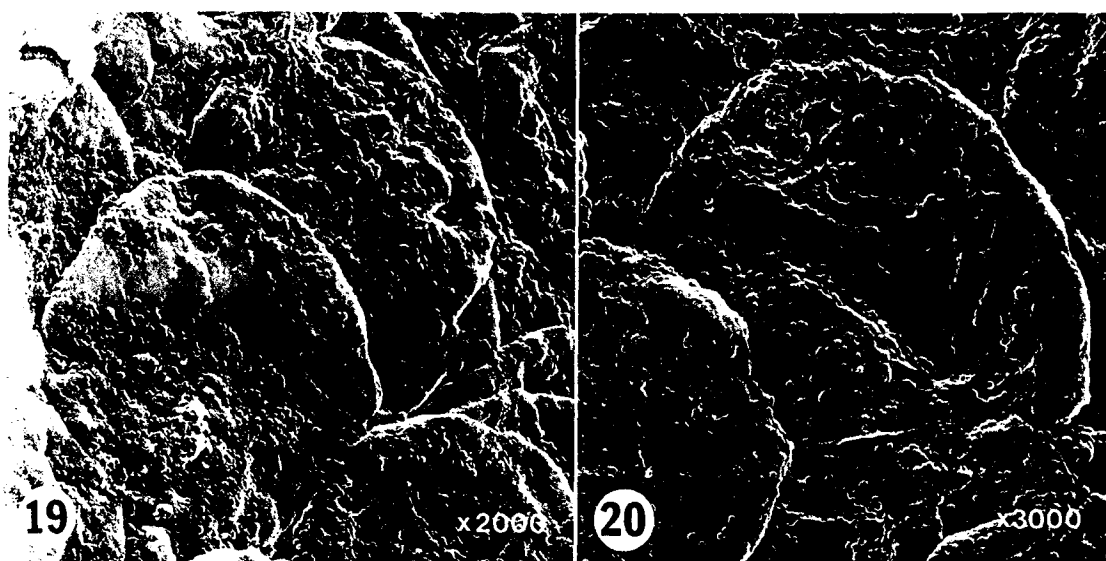


Fig. 19, 20. Scanning electron micrographs of porate pollen with verrucate sculpture from an anther of the staminate flower shown in Fig. 17. 19. $\times 2,000$. 20. $\times 3,000$.

Oligocene of Rott, West Germany, were studied in the collections of the University of Bonn (BONN courtesy H.-J. Schweitzer), the University of Cologne (KÖLN; courtesy E. K. Kempf), and the British Museum (Natural History)(V; courtesy C. R. Hill). Fruits from the Miocene of France were examined at the Museum National d'Histoire Naturelle de Paris (MNHN; courtesy C. Blanc). Those from the upper Eocene of Häring, Tirol, Austria, and from the upper Oligocene of Zagorje (Sagor), Yugoslavia, were studied at the Geologische Bundesanstalt, Vienna (GBV; courtesy F. Stojaspal), and at Naturhistorisches Museum of Vienna (NHMV; courtesy J. Kovar-Eder).

To obtain pollen, carbonaceous fragments were removed from the anther region of staminate flowers (Fig. 17), cleaned in HCl followed by HF, and macerated on a microscope slide using Schultzes solution, washed in water and cleared with ammonia. The resulting pollen masses were mounted on microscope slides with Protex medium for light microscopy (Fig. 18), and on aluminum stubs for analysis with a Cambridge StereoScan electron microscope (Fig. 19, 20). Attempts to analyze the pollen by TEM (courtesy W. L. Crepet) proved unsatisfactory because of extreme compaction of pollen grains in the single specimen available.

SYSTEMATICS—The following generic description is based upon material from both North America and Europe, especially on well preserved material from the Eocene Green River Formation of Utah and Colorado (Fig.

1–26), the lower Oligocene Florissant beds of Colorado (Fig. 27–44), and the upper Oligocene strata of Rott, West Germany (Fig. 46–48). Terminology for the description of leaves is adopted from Hickey (1973).

Cedrelospermum Saporta

Amended generic description—Twigs 2.5–8 cm long, with 4–10 leaves; distichous phyllotaxy (Fig. 1–4, 11, 27, 28, 33); internodes 3–12 mm, usually similar in length along much of each shoot. Axillary buds rounded, about 1 mm long; vernation conduplicate.

Leaves narrow, with length/width ratios of 2.1–9.5 ($\bar{x} = 4.6$), usually elliptical to ovate or lanceolate (Fig. 5–11, 33–39); 11–68 ($\bar{x} = 37$) mm long and 2.1–23 ($\bar{x} = 8.7$) mm wide. Apex acute, attenuate; base acute with cuneate to rounded sides, nearly symmetrical to markedly asymmetrical. Petiole stout and relatively short (2–5 mm), often bent at junction with lamina. Margin occasionally entire but typically serrate, with simple teeth, distributed one per secondary vein. Teeth occurring along the full length of the lamina, or confined to the upper two-thirds to one-third of the lamina (Fig. 1, 5); teeth ranging from prominent in some leaves to small in others, and typically better developed in the upper two-thirds of the lamina. Tooth apices typically obtuse or right-angled blunt or rounded, nonglandular. The principal vein of each tooth is a secondary vein that enters the tooth submedially (Fig. 12, 13, 40).

Venation pinnate; midvein stout, straight to

curved. Secondary veins strong, craspedodromous, more or less parallel, arising from the midvein at angles of 40–60°, all about equal in strength, regularly spaced, 8–21 pairs, uniformly curved toward the margin. Secondaries typically giving off a strong exmedial branch near the margin that is directed to the tooth sinus and along the apical flank of the tooth to the tooth apex (Fig. 12, 13, 40); this branch particularly prominent in the European species. Secondary veins terminating in teeth or, where the margin is entire, sweeping upward and thinning along the margin, losing identity on approaching the superadjacent secondary. Inter-secondary veins present, up to 5 on each side of the midvein, but rarely extending more than one-third of the distance to the margin. Tertiary veins strong, typically percurrent (North American species) to disorganized (European species). Quaternary and quinary veins strongly impressed. Highest order of venation with excurrent branching is the fifth. Areoles quadrangular to polygonal, 0.25–1.0 mm; freely ending veinlets simple, curved, branched 1 to 3 times.

Flowers unisexual, axillary in cymes of 3–5 (Fig. 14–17). Anthesis and fruit development occurring with leaves expanded. Perianth thin and rarely preserved, hypogynous with approximately 5 shallow lobes. Staminate flowers (Fig. 17) with about 4–6 stamens, consisting of anthers 1.1–1.4 mm long with longitudinal dehiscence; filaments short or absent. Pollen (Fig. 18, 19) is subrounded in equatorial outline, 18–24 μ m in equatorial diameter and about 3–5-porate with sculpture consisting of fine scabrae distributed over a rugulate exine surface.

Fruits samaroid, nonstipitate, borne on ebracteate pedicels 0.5–1.2 mm long (Fig. 21). Perianth inconspicuous (Fig. 26, 46, 47) with about 5 lobes sometimes persisting at the proximal end of the fruit. Samaras 5.5–11.0 (\bar{x} = 7.6) mm long and composed of a thin elliptical endocarp 2–6 (\bar{x} = 4) mm long and 1.3–4 (\bar{x} = 2.3) mm wide, adjoined laterally by a large primary wing and (in most specimens of the North American species) a small secondary wing (e.g., Fig. 22). Primary wing elongate, 2.0–3.6 (\bar{x} = 2.9) mm wide and oriented oblique (10–40°) to the long axis of the endocarp with 5–7 subparallel veins (including marginal veins) approximately equal in thickness that converge toward a stigmatic area at the distal, adaxial margin. Occasional finer veins forming cross-ties or running sinuously between the thick veins. Secondary wing (present only in American species; Fig. 21–26, 29, 41–44) markedly smaller, 0.3–0.9 mm long, 0.3–0.7 mm wide,

subtriangular, oriented nearly parallel to the long axis of the endocarp, typically somewhat thicker than primary wing and without obvious venation. In the European species and in occasional specimens of the North American species where the secondary wing is absent, the stigmatic region of the primary wing distinctly cleft (Fig. 25, 45–47) with a suture line running between the cleft and the endocarp. Endocarp surface with reticulate ribbing (Fig. 26, 44, 47). Fruit abscission occurring at the top of pedicel; pedicel typically remaining attached to twig (Fig. 31).

Type species—Saporta (1889) did not specify a type species for *Cedrelospermum*. The first species named by him, *C. aquense*, is taken as the generic type. The holotype of *C. aquense*, a fruit from the upper Oligocene of Aix-en-Provence, France, is refigured photographically in Manchester (1987, pl. 1, fig. 4).

Nomenclature—Physical connections between leaves and fruits prove that these different plant parts were produced by the same genus of fossil plant although these organs have long held separate generic names. Additional names have resulted from the fact that the shared generic affinity of the European and American species long went unrecognized, resulting in separate generic assignments until recently (Manchester, 1987). Although MacGinitie (1974) proposed the generic name *Alafructus* based upon American specimens, the name *Cedrelospermum*, was published earlier (Saporta, 1889) and must be given priority. This name also has priority over others that have been applied to the dispersed fruits including *Embothrites* and *Banksites* (synonymy and discussion, Manchester, 1987).

Distinction of species—Two American species and at least one European species² of *Cedrelospermum* can be recognized on the basis of differences in fruit size and wing development and leaf serration and venation as indicated in the following key. Some intergra-

² In my previous treatment of *Cedrelospermum* (Manchester, 1987), I mistakenly referred all of the European fruits to *C. leptospermum* (Ettingshausen) Manch. Although the epithet *leptospermum* (Ettingshausen, 1855) was published prior to *C. aquense*, the later epithet has priority because it is the type species of Saporta's *Cedrelospermum*. It may be that the older, smaller fruits described by Ettingshausen represent a species distinct from *C. aquense*, for which the name *C. leptospermum* would be required, but larger collections of the fruits, and a better understanding of associated foliage are necessary to evaluate this possibility.

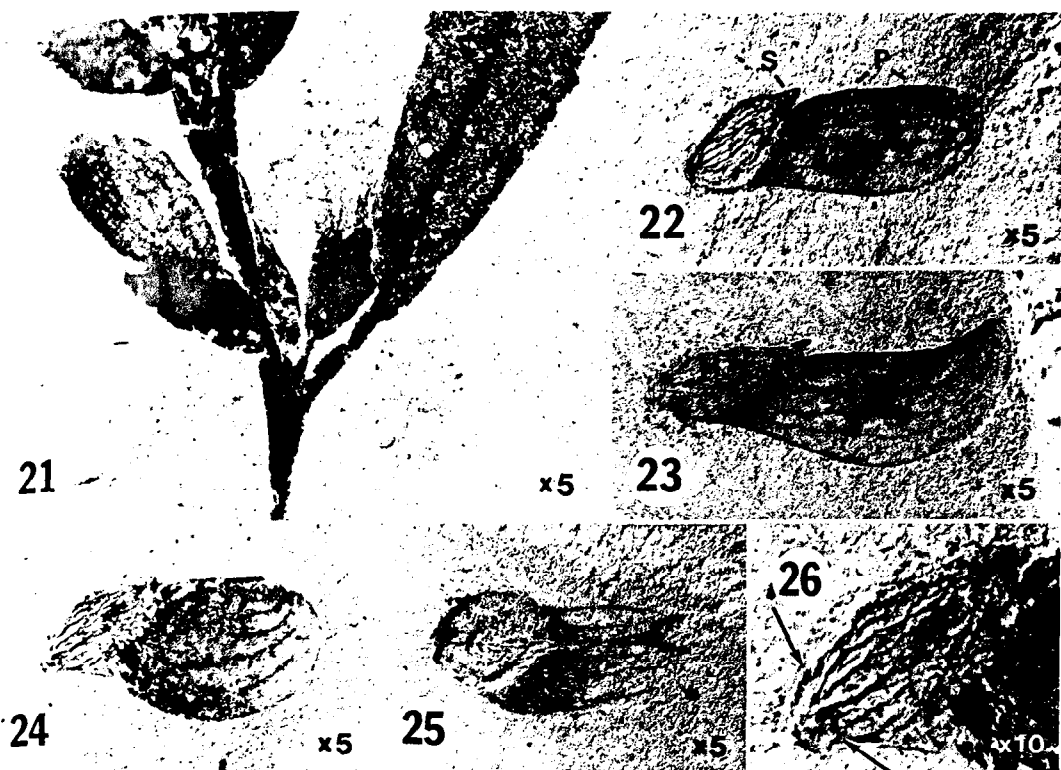


Fig. 21-26. *Cedrelospermum nervosum* fruits from the Green River Formation near Watson, Utah. Magnified $\times 5$ except as noted. 21. Detail from Fig. 2, showing three fruits attached by slender pedicels to the leaf axil. 22. Fruit showing the striated endocarp impression, the large primary (P) and small secondary (S) wing. As is typical, the marginal vein is approximately equivalent in strength to the other veins of the primary wing, IU 15753-7334. 23. One of the long primary wings observed for this species; contrast with fruits of *C. lineatum* from Florissant (Fig. 29, 41, 42); IU 15753-7335. 24. Specimen with a relatively broad primary wing and poorly developed secondary wing, IU 15753-7328. 25. Highly unusual specimen for this species, with a single wing (no secondary wing) having a distal stigmatic notch similar to that typical of the European species; compare with Fig. 45, 46; IU 15753-7337. 26. Detail from Fig. 24, showing shallow perianth at the base (arrows), and striations of the endocarp. $\times 10$.

dation occurs, such that some leaves or fruits from the Green River Formation may resemble those from Florissant and vice versa, but the normal leaves and fruits of each species are readily distinguished by characters comparable to those used in distinguishing modern species of elms.

1a. Fruits normally with two wings, one large and prominent, the other very reduced, stigmatic area positioned along the distal, adaxial surface of the primary wing, not confined to a notch. 2

2a. Fruits small, almost always less than 1 cm long, leaves usually not markedly asymmetrical, frequently partially or completely entire-margined, teeth often blunt to rounded (type stratum: Eocene Green River Formation *Cedrelospermum nervosum* (Newb) Manch. comb. nov.

2b. Fruits large, usually greater than 1 cm

long, leaves usually markedly asymmetrical, always serrate, teeth prominent, frequently sharp (type stratum: Oligocene Florissant beds)

. *Cedrelospermum lineatum* (Lesq.) Manch. 1987.

1b. Fruits with only one wing, stigmatic area confined to a notch at the distal wing margin (late Eocene to Miocene of Europe *Cedrelospermum aquense* (Saporta) Saporta.

***Cedrelospermum nervosum* (Newberry)
comb. nov (Fig. 1-26)**

Basionym—*Planera nervosa* Newberry 1883, p. 508; 1898, p. 82, pl. 67, fig. 2, 3.

Amended species description—Twigs up to 2.5-8 cm long, with 4-10 leaves; internodes 3-12 mm long. Leaves narrow elliptical (with the widest part midway between the base and apex) to ovate or lanceolate, with the widest

part typically one-third to one-half of the distance from the base to the apex; leaves 11–65 (\bar{x} = 34; N = 81; SD = 12.9) mm long, 2.1–23 (\bar{x} = 8.5; N = 81; SD = 4.7) mm wide, with length/width ratios 2.1–9.5 (\bar{x} = 4.6; N = 81; SD = 1.4). Apex acute, attenuate, base acute with cuneate to rounded sides, nearly symmetrical to asymmetrical. Petiole 1.7–6.5 (\bar{x} = 3.5; N = 63; SD = 1.12) mm long. Leaf margin variable from entire to serrate. Serrate leaves with simple teeth, distributed one per secondary vein; teeth occurring along the full length of the lamina, or confined to the upper two-thirds to one-third of the lamina. Teeth obtuse or right-angled, blunt or rounded, less frequently sharp, typically with a convex upper flank and convex outer flank. Venation pinnate; midvein stout, straight to curved. Secondary veins regularly spaced, 6–18 (\bar{x} = 10; N = 44; SD = 3.6) pairs, uniformly curved toward the margin, terminating in teeth or, where the margin is entire, sweeping upward and thinning along the margin, losing identity on approaching the superadjacent secondary, not forming prominent marginal loops. Tertiary veins sinuous, often oppositely and alternately percurrent, oriented at right, or somewhat obtuse angles, to midvein. Higher order venation forming a regular, more or less orthogonal mesh; highest order with excurrent branches 5th. Areoles 4-sided to polygonal. Freely ending veinlets simple, straight to curved, or branched once or twice.

Flowers unisexual, axillary in fascicles of 3–5. Anthesis and fruit development occurring on new wood, with intact leaves. Perianth thin and rarely preserved, number of lobes uncertain. Staminate flowers with about 4–6 tetralocular stamens per flower, consisting of anthers 1.1–1.4 mm long with longitudinal dehiscence; filaments short or absent. Pollen subrounded, 18–22, \bar{x} = 20 μ m with 4–5 pores and rugulate with fine scabrae.

Samaras 4.4–11.0 (\bar{x} = 7.5; N = 28; SD = 1.3) mm long and 1.9–4 (\bar{x} = 2.9; SD = 0.45) mm wide, borne on pedicels 0.5–1.2 mm long; endocarp thin, oval 2–3.5 mm long and 1.3–2.6 mm wide adjoined by 2 (rarely 1) lateral, asymmetrical wings (Fig. 21–24): the primary wing elongate, oriented oblique to the long axis of the seed with 5–7 subparallel veins, including marginal veins, approximately equal in thickness that converge toward a stigmatic area at the distal, adaxial margin. The secondary wing much smaller than the primary, 0.3–0.9 mm long, 0.3–0.7 mm wide, subtriangular oriented nearly parallel to the long axis of the seed, often somewhat thicker than the primary wing and without obvious venation. In rare

cases where the secondary wing is absent (Fig. 25), the stigmatic region of the primary wing is distinctly cleft. Endocarp surface reticulate, with wrinkles oriented parallel to the long axis of the endocarp (Fig. 22, 26).

Material—The above description is based strictly upon material from the middle Eocene Parachute Creek Member of the Green River Formation, from which the mutually attached leaves, flowers and fruits were obtained. Localities include IU 15751, 15753, 15754, 15755, 15883, 15884, 15885, USGS 8773, near Watson, Uintah County, Utah; UCMP-PA106, IU 15727, 18001 from Wardell Ranch, Rio Blanco County, Colorado, and USGS 8642 on Carr Creek, Garfield County, Colorado.

Specimens with attached leaves and fruits include IU7043 (Fig. 1, 6), IU7041 (Fig. 2), IU7044 (Fig. 4, 5), IU7347, and USNM 38590 (Fig. 3). Specimens with attached flowers include IU7042 (Fig. 14, 16) and USNM 414096 (Fig. 15, 17). One nonreproductive twig of leaves is known (IU7308; Fig. 11). More than 45 fruits were examined, including 33 at IU (including IU7326–7345), 9 at USNM, and 5 at UCMP. In addition to USNM 7307, here designated the lectotype (Fig. 8), more than 80 isolated leaves were examined, including 70 at IU (including IU 7349–7353), and 11 at USNM.

The following published leaf records from the Green River Formation conform to this species: *Planera nervosa* (Newberry, 1898, p. 82, pl. 67, fig. 2, 3; Brown, 1929, pl. 71, fig. 7–9); *Myrica praedrymeja* Knowlton (1923, p. 157, pl. 36, fig. 1–3); *Myrica minuta* Knowlton (1923, p. 157, pl. 37, fig. 12; Brown, 1934, p. 54, pl. 9, fig. 1, 2); *Salix lineara* Knowlton (1923, p. 155, pl. 37, fig. 8); *Rhus myricoides* Knowlton (Brown, 1929, p. 287, pl. 73, fig. 9); *Zelkova nervosa* (Newberry) Brown (1946, p. 346; MacGinitie, 1969, p. 99, pl. 5, fig. 2, 5, pl. 10, fig. 2, 4, pl. 23, fig. 4).

In addition, the following citations of fruits from the Green River Formation conform to this species: *Banksites lineatulus* Cockerell (1925, p. 8, pl. 2, fig. 3); *Lomatia lineatulus* (Cockerell) MacGinitie (1969, p. 99, pl. 16, fig. 6, 7); *Cedrelospermum lineatum* (Lesq.) Manch. (Manchester, 1987, pl. I., fig. 5–7, 9, only).

Discussion—*Cedrelospermum nervosum* branchlets with attached leaves and fruits occur in the middle Eocene Parachute Creek Member of the Green River Formation in Utah and Colorado. Isolated leaves and fruits are abundant in the same horizon, and MacGinitie (1969, 1974) calculated that this species was the second most abundant leaf type in the

Eocene Uinta Lake. Although less abundant in localities outside the Green River Formation, isolated leaves and fruits that appear to conform to *C. nervosum* occur in the early middle Eocene Kisinger Lakes flora of the Absaroka Province of Wyoming (MacGinitie, 1974) and in the middle to late Eocene Clarno Formation of Oregon (West Branch Creek, and Gosner Road localities; Manchester, 1987, and unpublished data).

Leaves of *Cedrelospermum nervosum* are highly variable in marginal character, size and shape. The extent of this variability, which previously could only be deduced from suites of detached leaves, can now be confirmed by the variation of leaves on whole branches (Fig. 14, 11). The presence of occasional entire-margined leaves in *C. nervosum* is proved by their attachment to twigs that also bear the more typical serrate leaves, and characteristic fruits (Fig. 1). Such leaves were not previously included in the concept of this species. The reproductive branches recovered so far have relatively small leaves 12–29 mm long; but leaves of the vegetative shoot (Fig. 11) reach larger dimensions of 27–40 mm. It is therefore likely that many of the larger isolated leaves represent foliage of mature vegetative branches. Comparable size dimorphism occurs in extant *Zelkova* (Burnham, 1986).

Two twigs with intact axillary flowers (Fig. 14, 1) indicate that the flowers were unisexual and that flowering occurred with the leaves fully expanded. These bear the same kind of leaves as the fruiting twigs. One of the specimens appears to be pistillate, with up to 3 pedicels per leaf axil, each terminated by a lamellar structure (Fig. 16), about 1.0 mm long and thickened along one lateral margin, interpreted to represent the incipient fruit wing. No stamens appear to be present on any of the flowers of this twig. The other specimen shows exclusively staminate flowers (Fig. 17), 3–4 in the axil of each leaf. The 4 to 6 stamens of each flower are tightly clustered, each about 1.1–1.4 mm long. Perianth parts are not preserved in either of the flowering shoots, and are interpreted to have been relatively thin.

Masses of pollen are preserved within the stamens (Fig. 18–20). Although the pollen is highly compressed, it is clearly porate and has sculpture consisting of closely spaced fine scabrae over a rugulate surface. Individual grains could not be dislodged from the compressed pollen masses, and on most grains, it is difficult, both with light microscopy and with SEM, to resolve the number of pores. However, from the few grains for which pore number could be observed, and from the number of angles on

polygonal grains, the number of pores is clearly variable and probably ranges from 3–5 pores per grain (Fig. 19, 20).

The fruits of this species are quite uniform in morphology, generally consisting of both a large primary wing and a small secondary wing (Fig. 21–24); however, out of 43 specimens from the Green River Formation one specimen was found that lacks the secondary wing and bears a distal stigmatic cleft (Fig. 25). This is the normal condition for fruits of the European species (Fig. 45–47) and has been observed occasionally in populations from the Clarno Formation of Oregon (Manchester, 1987).

Cockerell (1925) was the first to distinguish the Green River fruits of *Cedrelospermum* (then placed in *Banksites*) as a separate species from those of the younger flora at Florissant. Noting that these fruits are “smaller and presumably a different species,” from those described previously by Lesquereux (1883) as *B. lineata* from Florissant, he coined the epithet *lineatulus* for the Green River disseminules. In my recent treatment of isolated fruits from North America and Europe (Manchester, 1987), I recognized only one species for the American fruits, believing that the size difference was insignificant, and thus placed specimens from the Green River and Clarno formations together with the Florissant species. Having now studied larger populations of fruits both from Florissant and Green River, I believe there is a good basis for maintaining Cockerell’s distinction although the epithet *nervosum* (Newberry, 1898) takes priority over *lineatulus*. Table 1 compares fruit and leaf dimensions for specimens from the Green River and Florissant collections. Qualitative differences in the attached foliage, discussed in the next section, also support the recognition of this Eocene Green River species as distinct from the Oligocene Florissant species.

***Cedrelospermum lineatum* (Lesq.) Manch.**
1987 (Fig. 27–42)

Basionym—*Banksites lineatus* Lesquereux (1883, p. 165, pl. 32, fig. 21.)

Amended species description—Twigs 2.5–8 cm long, with 4–10 leaves, internodes 3–12 mm. Leaves usually narrow ovate or lanceolate, with the widest part usually one-fourth to one-third of the distance from the base to the apex, rarely elliptical; lamina 11–68 (\bar{x} = 40; N = 110; SD = 13.4) mm long and 3.2–21 (\bar{x} = 8.9; N = 110; SD = 3.2) mm wide; length/width ratios 2.5–8.6 (\bar{x} = 4.6; N = 110; SD = 1.1). Apex acute, attenuate, base acute, usually markedly asymmetrical to almost symmetri-

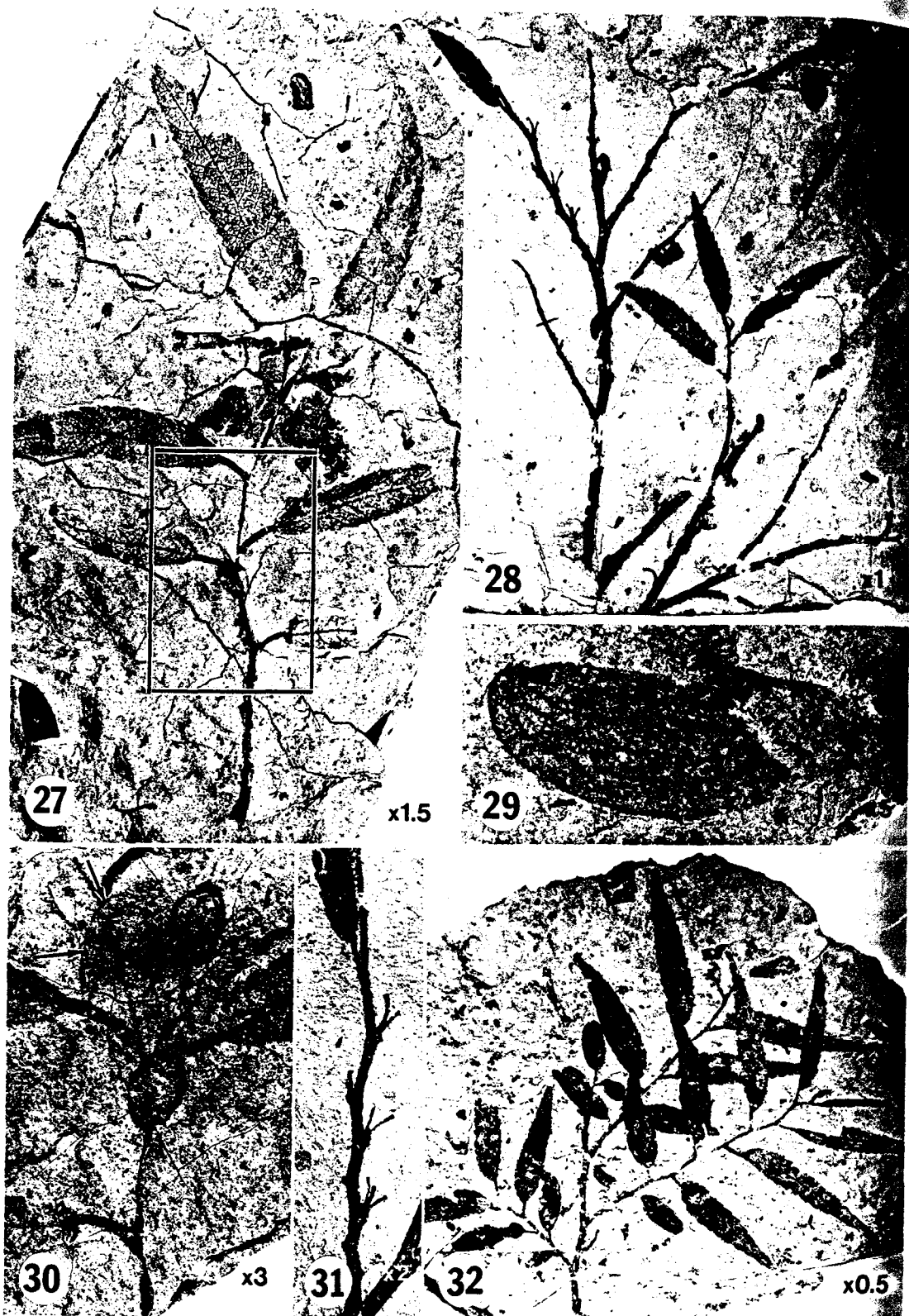


Fig. 27-32. Branches with leaves and fruits of *Cedrelospermum lineatum* (Lesq.) Manch. from the lower Oligocene Florissant flora, Colorado. 27. Twig showing distichous phyllotaxy and well-preserved leaves. Rectangular outline indicates position of attached fruits enlarged in Fig. 30, YPM Pb25232. $\times 1.5$. 28. Specimen showing three orders of branching, with the fruits and most of the leaves shed, YPM Pb25244. $\times 1$. 29. Lectotype of *Cedrelospermum lineatum* (Lesq.) Manch., originally figured as *Banksites lineatus* (Lesquereux, 1883), showing distinctive venation of fruit wing.

TABLE 1. Comparison of fruit and leaf dimensions for different species of *Cedrelospermum*^a

	<i>C. nervosum</i> ^b	<i>C. lineatum</i> ^c	<i>C. aquense</i> ^d
Fruits			
Number measured	43	28	25
Fruit length, mm	4.4–11 (7.5)	9–14.5 (11.2)	6.5–14.0 (11.0)
SD	1.29	1.34	2.05
Fruit width, mm	1.9–4.0 (2.9)	2.2–5.5 (4.2)	3.0–6.0 (4.6)
SD	0.45	0.69	0.83
Endocarp length, mm	1.5–4 (2.9)	3.2–5.0 (4.2)	2.0–6.0 (4.3)
SD	0.44	0.51	0.85
Endocarp width, mm	1.0–2.6 (1.7)	2.0–3.8 (2.5)	1.5–4.0 (2.7)
SD	0.33	0.38	0.55
Leaves			
Number measured	81	110	—
Leaf length, mm	11–65 (35)	11–68 (40)	
SD	12.9	13.4	
Leaf width, mm	2.1–23 (8.5)	3.2–21 (8.9)	
SD	4.66	3.21	
Length/width ratio	2.1–9.5 (4.6)	2.5–8.6 (4.6)	
SD	1.42	1.06	

^aincluding range (and mean).

^bFrom the Middle Eocene Parachute Creek Member of the Green River Formation, Utah and Colorado.

^cFrom the early Oligocene Florissant beds, Colorado.

^dFrom the late Oligocene of Rott, West Germany.

cal. Petiole 1.8–6.0 mm long. Leaf margin prominently serrate with simple teeth beginning near the base; no entire-margined leaves observed. Teeth with right angle apices that typically are not rounded, usually with a straight upper flank and straight to slightly concave (less commonly convex) outer flank. Secondary veins regularly spaced, 8–21 pairs, uniformly curved toward the margin and terminating in teeth. Tertiary veins typically percurrent, or semireticulate, oriented at right or obtuse angles to the midvein. Higher order venation forming a regular, more or less orthogonal mesh; highest order with excurrent branching 5th. Areoles 4-sided to polygonal. Freely ending veinlets once to twice branched, straight, or curved.

Samaras 9–14.5 (\bar{x} = 11.2; N = 28; SD = 1.34) mm long and 2.2–5.5 (\bar{x} = 4.2; N = 28; SD = 0.69) mm wide, borne on pedicels 2.0–3.0 mm long; endocarp thin, elliptical 3.2–5 (\bar{x} = 4.2; N = 28; SD = 0.51) mm long and 2.0–3.8 (\bar{x} = 2.5; N = 28; SD = 0.38) mm wide, adjoined by 2 lateral wings: the primary wing is oriented oblique to the long axis of the seed and possesses 6–8 subparallel veins, including marginal veins, of approximately equal thick-

ness, that converge toward a stigmatic area at the distal, adaxial margin. Secondary wing minute, subtriangular, oriented nearly parallel to the long axis of the seed, often somewhat thicker than primary wing and without obvious venation. Some specimens showing only vestigial secondary wing and concave stigmatic area. Endocarp surface reticulate.

Material—The above description is based strictly upon material from the lower Oligocene Florissant beds, from which mutually attached leaves and fruits were obtained. Specific localities include IU 15877, 15880, and UCMP 3731, 3732, 3733 in Teller County, Colorado.

Branches with attached leaves and/or fruits include YPM-PU 25232 (Fig. 27, 30), YPM-PU 25244 (Fig. 28, 31), USNM 387542 (Fig. 32), YPM-PU 25236 (Fig. 33), USNM 331732, 50237, 331805, 331814, 331825, 332848. Isolated fruits include the lectotype (USNM 1781, Fig. 29) and 2 others at USNM, 5 at IU [including IU 7275 (Fig. 41), IU 7274 (Fig. 42), IU 7273, 7276, 7307], 3 at FM (including P23076, P23085, P23073), 6 at UCMP (including UCMP 3665–3667 + uncat.), 2 at MSU, 4 at UCM, 1 at DNHM, and 1 at WC. Isolated

USNM 1781. $\times 5$. 30. Counterpart of specimen in Fig. 27, showing faintly preserved fruit of *C. lineatum*; arrows indicate margin of fruit wing; for comparison with Fig. 29. $\times 3$. 31. Detail of twig in Fig. 28, showing two to three persistent fruit pedicels at each node. $\times 2$. 32. Vegetative branch with three lateral twigs and typical leaves larger than those of the fruiting twigs (Orig. Lesq. 1883, pl. 26, fig. 5), USNM 387542. $\times 0.5$.

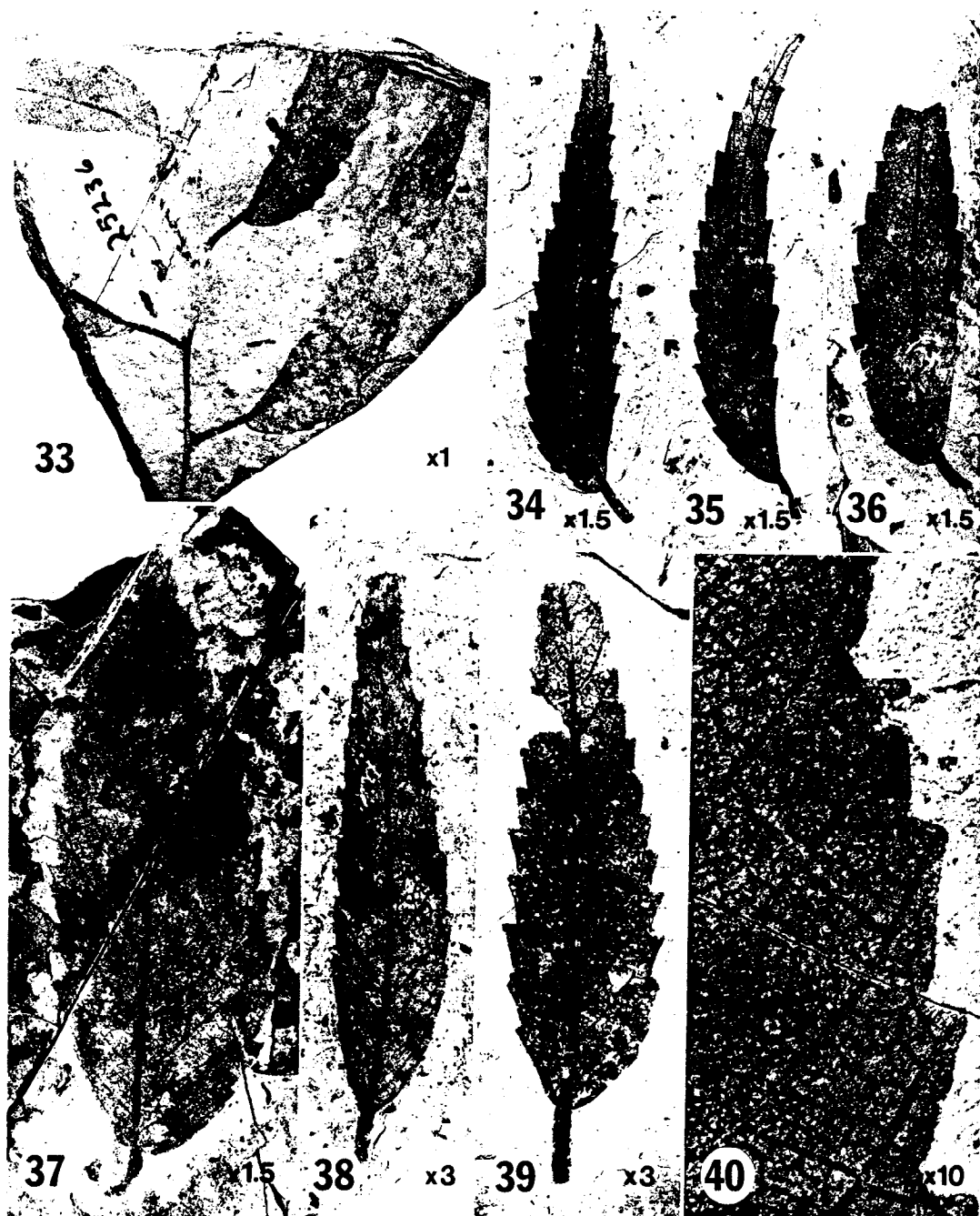


Fig. 33-40. Variation in leaves of *Cedrelospermum lineatum* from Florissant, Colorado. 33. Vegetative twig showing distichous phyllotaxy, asymmetrical leaves and small axillary buds, YPM-Pb25236. $\times 1$. 34. Typical leaf, asymmetrical with prominent, sharp right-angle teeth, and stout petiole, IU 15880-7277. $\times 1.5$. 35. Another example IU 15880-7279. $\times 1.5$. 36. Leaf with obtuse, blunt teeth uncommon for this species, IU 15880-7284. $\times 1.5$. 37. Large, broad ovate leaf with well-preserved venation, IU 15880-7297. $\times 1.5$. 38. Small leaf atypical for this species in being nearly symmetrical and in lacking prominent teeth in the basal $\frac{1}{3}$ of the lamina, IU 15880-7287. $\times 3$. 39. Small leaf with typical prominent teeth and strong craspedodromous secondary veins, IU 15880-7286. $\times 3$. 40. Counterpart of specimen in Fig. 33, magnified to show venation. Note that the secondary veins are often convexly curved upon entering the tooth. Sinuses of the teeth are braced by strong tertiary veins. Tertiary veins are mostly percurrent. $\times 10$.

Leaves examined include 26 at IU (including IU 7277-7306, Fig. 34-40), 10 at MSU, 27 at FM, 42 at USNM, 19 at DMNH, and about 25 at UCMF.

The following published citations of leaves from Florissant represent *Cedrelospermum lineatum*: *Rhus* (?) *drymeja* Lesquereux (1874, p. 416); *Callicoma microphylla* ? Ett. (Lesquereux, 1878, pl. 43, fig. 2-4); *Myrica drymeja* (Lesq.) Knowlton (1898, p. 146; Cockerell, 1910, p. 40, fig. 5); *Myrica acuminata* Lesq. [not Unger] (1878, p. 130, pl. 17, fig. 2, 3 only); *Myrica callicomaefolia* Lesquereux (1878, p. 146, pl. 26, fig. 5-14); *Zelkova* Morphotype B (Burnham, 1986, p. 154, pl. 1, fig. 3, 5).

In addition, the following citations of fruits from Florissant represent *C. lineatum*: *Banksites lineatus* Lesquereux (1883, p. 165, pl. 32, fig. 21); *Lomatia lineata* (Lesq.) MacGinitie (1933, p. 108, pl. 34, fig. 4-6); *Cedrelospermum lineatum* (Lesq.) Manchester (1987, p. 124, pl. 2, fig. 9).

Discussion—This species is a common and distinctive component of the early Oligocene Florissant flora, and is the second most abundant leaf type in the assemblage (MacGinitie, 1953). The species is also represented by fruits (Fig. 43, 44) and foliage (IU 8026) in the Oligocene Catahoula Formation of Texas. The latter locality, from which a diverse angiosperm flora is being investigated (Daghlian, Crepet, and Delevoryas, 1980), represents the easternmost occurrence of *Cedrelospermum* known in North America.

Two Florissant specimens confirm the conspecificity of fruits and leaves of *Cedrelospermum lineatum*. One is a twig of eight leaves showing two faintly preserved samaras at the junction between one of the leaves and the twig, apparently in axillary position (Fig. 27, 30). The other specimen shows attached pedicels of fruits that have been shed (Fig. 28), and confirms the axillary position and cymose inflorescence type. Two to three ebracteate pedicels are visible at each node (Fig. 31), and it is possible that 1 or 2 additional pedicels could be hidden by sediment.

Within the range of variation in *C. lineatum* foliage, some individual leaves could be difficult to distinguish from some leaves of *C. nervosum*. Previous suggestions that the two species can be distinguished on the basis of size (MacGinitie, 1969) are not clearly supported by the statistics for the larger sample sizes now available (Table 1). However, I agree with Brown (1946) and MacGinitie (1969) that the Florissant leaf impressions tend to be more

inequilateral and falcate in shape; and the marginal dentations are more angular than in the Green River species. In addition, all leaves of *C. lineatum* are serrate along most of their length, whereas those of *C. nervosum* vary from serrate to entire-margined. The teeth are frequently more angular in *C. lineatum* leaves than in those of *C. nervosum*, and the secondary veins commonly bend convexly as they enter the teeth in *C. lineatum* (Fig. 40) but usually bend concavely upon entering the teeth of *C. nervosum* (Fig. 12, 13).

In addition to the reproductive branches, the collections from Florissant include large sections of vegetative branches. Examples are illustrated in Cockerell (1910, p. 42) and in Fig. 32, 33. The leaves of vegetative branches are generally larger and more asymmetric than those of fruit bearing branches.

COMPARISON WITH EUROPEAN MATERIAL—In Europe *Cedrelospermum* ranges stratigraphically from the late Eocene (e.g., Häring, Austria) to the late Miocene (e.g., Randecker Maar, West Germany) and was geographically widespread, with localities in France, West Germany, East Germany, Austria, Yugoslavia, Czechoslovakia, and Hungary (Rüffle, 1963, sub *Embothrites borealis*; Manchester 1987, sub *Cedrelospermum leptospermum*).

Assignment of the American species considered in this paper to a genus initially established from European fossils follows from careful comparison of specimens from both continents (Manchester, 1987). *Cedrelospermum* is diagnosed on the basis of fruits (Saporta, 1889; Manchester, 1987), and as yet no specimens from Europe show a connection with foliage. However, the utility of fruit characters in generic taxonomy of extant Ulmaceae (Manchester, in press) supports the validity of using such characters to evaluate the congeneric status of the American and European fossils considered here. The generic name *Alafructus* formerly proposed for the American fruits (MacGinitie, 1974) is regarded as a junior synonym of *Cedrelospermum*, but could have utility at the subgeneric rank depending on the results of more intensive multiple-organ investigations of the European species.

European *Cedrelospermum* fruits (Fig. 45-47) are similar to those from North America in dimensions (Table 1), shape, orientation and venation of the wing, oval shape and ribbed sculpture of the endocarp, and occasional persistence of a small perianth. The wing venation, including a marginal vein and 5-7 subparallel veins that converge toward a distal stigmatic

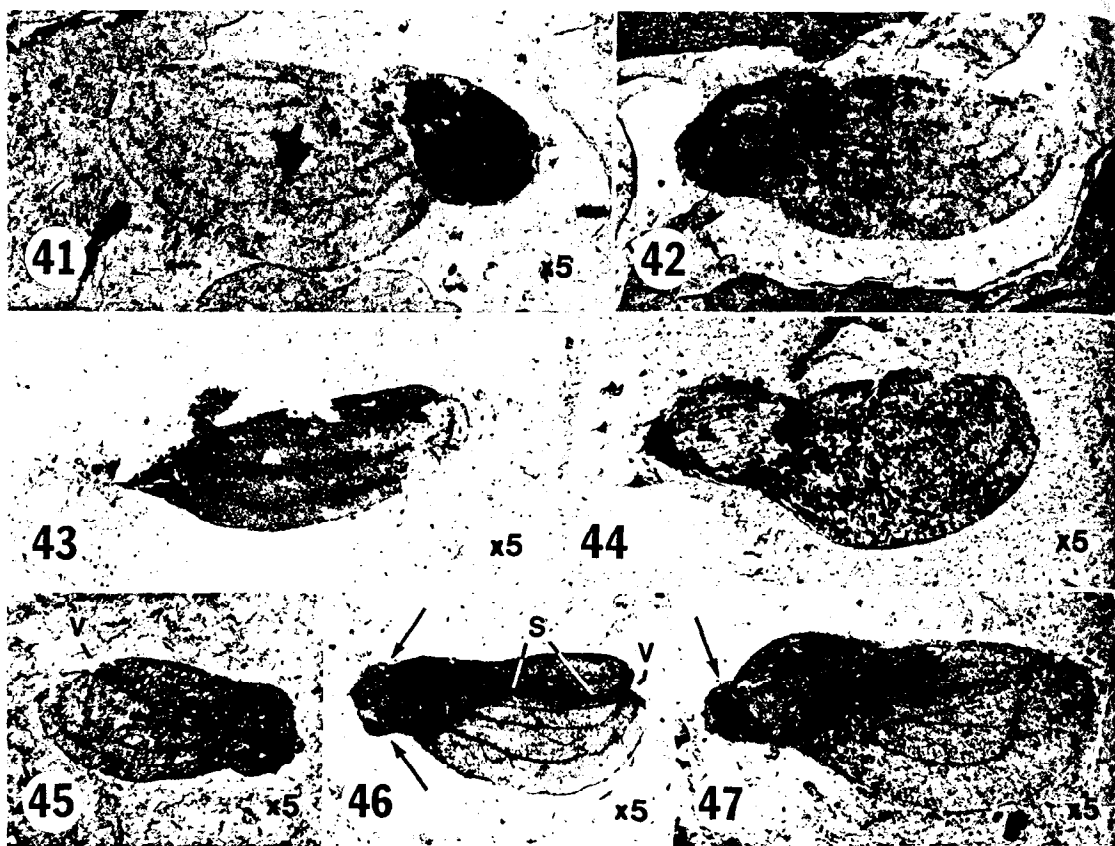


Fig. 41-47. Fruits of *Cedrelospermum* from the Tertiary of Colorado, Texas, Germany, and Czechoslovakia. All $\times 5$. Fig. 41, 42. Typical specimens of *C. lineatum* from Florissant, Colorado, contrasting by their larger size with typical fruits of *C. nervosum* (Fig. 21-26). 41. IU 15880-7275. 42. IU 15880-7274. Fig. 43, 44. *Cedrelospermum lineatum* fruits from the Oligocene Catahoula Formation, near Huntsville, Texas. 43. Specimen with relatively well-developed secondary wing. IU 8024. 44. Specimen showing striations of the endocarp impression. IU 8025. 45. *Cedrelospermum aquense*, (orig. *Embothrites leptospermum* Ettingshausen, 1855, pl. 14, fig. 21), from Häring, Austria, with characteristic V-shaped stigmatic notch (V) distally and absence of a secondary wing (cf. Fig. 22, 43); the small size is typical for this late Eocene locality. NHMV. Ett. #13. Fig. 46-48. Specimens of *C. aquense* from the late Oligocene of Rott, West Germany, BONN Coll. 46. Unusually small specimen for this locality; note the prominent suture line (S) leading to the well-developed stigmatic notch (V) at the distal end of the wing, and bulge at the proximal end of the endocarp indicating position of the perianth (arrows). 47. Specimen showing persistent perianth (arrow), and well-preserved reticulate sculpture of the endocarp.

area, with only occasional crosssties, is also similar between these species. The only morphological difference that I am aware of is that all of the European specimens (including those illustrated previously in the literature and about 35 that I have observed in the collections of BONN, KOLN, MNHNP, GBV, NHMV, and BM) lack the secondary wing, but have a well developed stigmatic cleft in the primary wing (Fig. 45-47). The presence of a small secondary wing and the absence of a well-developed stigmatic cleft is a characteristic feature of both of the American species (Fig. 21-24, 29, 41-44). However, among the American populations of *C. nervosum* and *C. lineatum*, there are occasional specimens that resemble the European specimens in the absence of a secondary wing,

and presence of a good stigmatic cleft (Fig. 25; Manchester, 1987, pl. II, fig. 4, 6, 7), a phenomenon supporting the conclusion that these species should be placed in the same genus.

Based on similarity with the attached American foliage and on evidence of association at localities where *C. aquense* fruits have been collected, *Tremophyllum tenerrimum* (Weber) Ruffle appears to be a likely candidate for the kind of leaf that was produced by the European species of *Cedrelospermum*. Ruffle (1963) established the foliage genus *Tremophyllum* and assigned it to the Ulmaceae based on comparison with the extant celtoid genus *Trema*. Ruffle observed similarities of small size, asymmetrical leaf shape, serration and tertiary venation between the fossil and *Trema*. How-

ever, *Tremophyllum* leaves are more similar to those of the Ulmoideae in the true pinnate venation and in the presence of only one tooth per secondary vein. *Tremophyllum tenerrium* leaves co-occur with fruits of *Cedrelospermum aquense* at the Oligocene of Rott and Miocene of Randecker Maar, West Germany.

Tremophyllum tenerrium leaves resemble those of the American *Cedrelospermum* species in the shape, size, spacing of simple teeth, and obtuse often blunt teeth. Indeed, Lesquereux (1878) recognized this when he assigned specimens from Florissant with a question mark to "*Callicoma microphylla*," the name that Ettingshausen (1855) applied to the specimens from the late Oligocene of Zagorje (Sagor), Yugoslavia. Nevertheless, they are distinct in some important respects. The secondary veins each give off a branch to the sinus that is more prominent than those of the American species. In addition, the arrangement of tertiary veins is more or less random in *T. tenerrium* (Weyland, 1938, pl. 7, fig. 13), in clear contrast to the percurrent pattern of *C. nervosum* and *C. lineatum*.

SYSTEMATIC POSITION OF CEDRELOSPERMUM—Knowledge of several organs of *Cedrelospermum*, including leaves, flowers, pollen and fruits, provides a rare opportunity for precise reconstruction (Fig. 48) and for detailed multiple-organ comparison between a fossil dicotyledon and its living relatives. The combination of distichous phyllotaxy, elliptical to lanceolate, often asymmetrical leaves, with nonglandular teeth and short stout petioles, flowers borne in axillary fascicles, superior, bicarpellate ovaries, fruits with a persistent stigmatic area along part of the wing and porate pollen with verrucate ornamentation confirms the position of *Cedrelospermum* within the Ulmaceae. However, this fossil presents a unique combination of characters that distinguishes it as an extinct genus in the family (Table 2).

Extant Ulmaceae are divided into two subfamilies: the Ulmoideae, with about 6 genera and the Celtidoideae with about 10 genera. The subfamilies are distinguished by morphological characters of the leaves, flowers, fruits, and pollen and are distinct in their flavonoid chemistry (Giannasi, 1978). Some workers (e.g., Grudzinskaya, 1967) elevate the Celtidoideae to familial status, noting that the Celtidaceae resemble the Moraceae as closely as the Ulmaceae *sensu stricto*. For present purposes I am using the Ulmaceae in its traditional, broader sense. *Cedrelospermum* is placed firmly within the Ulmoideae and dif-



Fig. 48. Reconstruction of a fruiting branchlet of *Cedrelospermum nervosum*, \times about 2.

ferentiated from the Celtidoideae on the basis of leaf venation (pinnate, not pinnipalmate) fruit type (samara with flattened endocarps rather than drupe with globose endocarp) and pollen pore number (3–5 rather than 2–3) and ornamentation (scabrae distributed over rugulate, rather than over smooth, surface).

Table 2 compares *Cedrelospermum* with extant genera of the Ulmoideae in selected characters of foliage, flowers and fruits. Within the Ulmoideae, *Cedrelospermum* appears to be closest to *Zelkova*, *Hemiptelea*, and *Phyllostylon*. These genera, like *Cedrelospermum*, have asymmetrically developed, nonstipitate fruits and leaves with simple teeth. *Ulmus*, *Planera*, and *Holoptelea* differ from the fossil in having bilaterally symmetrical, stipitate fruits and leaves that are entire (*Holoptelea*) or that have compound teeth. *Cedrelospermum* also differs from *Ulmus* and *Planera* in having leaves with very little branching of the secondary veins (Burnham, 1986).

In view of the former practice of assigning American leaves of *Cedrelospermum* to *Zelkova*, a genus presently native to East Asia and

TABLE 2. *Morphological comparison of Cedrelospermum with extant genera of Ulmoideae and with extant Celtidoideae^a*

	<i>Cedrelospermum</i>	<i>Ulmus</i>	<i>Planera</i>	<i>Holoptelea</i>	<i>Zelkova</i>	<i>Hemiptelea</i>	<i>Phyllastylon</i>	Celtidoideae
Reproductive characters								
Flowers unisexual	+	—	—	—	+	—	+ (—)	+ / —
Flowering on new wood	+	±	+	+	+	+	—	+
Fruits stipitate	—	±	+	+	—	—	—	—
Pedicels bracteate	—	+	—	nd	—	nd	+	nd
Fruit winged	+	+	—	+	—	+	+	— (+)
Wing development asymmetrical	+	—	na	—	na	+	+	na / —
Endocarp thin, elliptical	+	+	—	+	—	—	+	—
Pollen sculpture rugulate	+	+	+	+	+	+	+	—
Pollen pore number ^b	3–5	4–5	4–5	4–5	4–5	6–7	5	2–3
Pollen size, μm^b	18–22 (20)	23–50	20–40 (35)	23–33 (27)	25–31 (28)	42–51 (47)	29–38 (34)	10–31
Vegetative characters								
Twigs with spines	—	—	—	—	—	+	—	— / +
Leaves with teeth	+ / —	+	+	—	+	+	+	+ / —
Teeth ≤ 1 per secondary vein	+	—	—	na	+	+	+	—
Length/width ratio, lamina	2.1–9.5 (4.6)	1.6–3.4 (2.3)	1.3–3.0 (2.0)	1.4–2.0 (1.7)	1.5–4.3 (2.4)	2.1–2.8 (2.4)	1.4–2.3 (1.9)	nd
(number of leaves measured)	190	31	19	17	39	17	17	
Basal secondary veins acrodromous	—	—	—	—	—	—	—	+ / —
Leaf base commonly cordate	—	+	+	—	+	—	+	+ / —
Secondary vein branching frequent ^c	—	+	+	—	—	—	—	—

^a + = character present; — = character absent; na = not applicable; nd = not determined.^b Data from Zavada, 1983.^c More than 4 per leaf; Burnham, 1986.

the Caucasus region, it is useful to underscore the leaf and fruit characters that differentiate these genera. Leaves of *Cedrelospermum* are narrow in comparison with those of *Zelkova*. Thus, the length-width ratios average about 4.6 (range 2.1–9.5) in *Cedrelospermum nervosum* and *C. lineatum*, but around 2.5 (range 1.5–4.3) in *Zelkova*, *Ulmus*, and other extant genera (Table 2). The leaves of all extant species of *Zelkova* are serrate with prominent teeth from base to apex. The teeth of *Cedrelospermum* leaves typically are not as prominent and, in *C. nervosum*, the teeth may be few or none (the margin may even be entire). The conspicuously winged, pedicellate fruits and thin elliptical endocarps of *Cedrelospermum* contrast with the nonwinged, sessile, globose endocarps of *Zelkova*. *Cedrelospermum* resembles *Zelkova* in having unisexual flowers; most other ulmoideae have bisexual flowers. In *Zelkova*, flowers lower on the reproductive twigs are usually staminate and those of the upper parts are usually pistillate. However, in *Cedrelospermum* the flowers of each twig are exclusively pistillate or staminate.

Hemiptelea, with a single extant species in northeastern China and Korea, has prominently toothed leaves and curved globose endocarps like those of *Zelkova* and has been included within *Zelkova* by some taxonomists (Airy Shaw, 1973). Unlike *Zelkova*, *Hemiptelea* has bisexual flowers and winged fruits. In addition, the single extant species of *Hemiptelea* is a shrub with prominent spines, whereas the three extant species of *Zelkova* are trees with unarmed branches. Spines have not been observed on twigs of *Cedrelospermum* and are absent in all other genera of the Ulmoideae, although they are present in some species of the Celtidoideae. *Hemiptelea* pedicels are articulated near the base such that the dispersed fruits usually retain part of the pedicel. In contrast, *Cedrelospermum* fruits were typically shed without the pedicel, leaving the complete pedicels attached to the twig. As in *Cedrelospermum*, the fruit wing of *Hemiptelea* is asymmetrical and has a prominent marginal vein (Manchester, 1987). However, the wing is more constricted, and veins across the expanse of the wing are absent or few in the modern genus.

Although fruits of the Central and South American genus *Phyllostylon* resemble those of *Cedrelospermum* in the presence of a small secondary wing and a thin elliptical endocarp, they are much larger, and the major wing has a very different venation pattern, consisting of numerous closely spaced, thin subparallel veins that do not converge upon a stigmatic region

(Manchester, 1987; in press). Leaves of *Phyllostylon* are comparable in characters of the margin to those of *Cedrelospermum*, but differ in their broader shape and frequently cordate bases. Although functionally unisexual like *Cedrelospermum*, the pistillate flowers of *Phyllostylon* bear stamens without pollen below the superior ovary (Pennington and Sarukhan, 1968).

EARLY DIVERSIFICATION OF THE ULMOIDEAE—*Cedrelospermum* is sufficiently well understood morphologically that it should be taken into account as well as the extant genera in considering the history and evolution of the Ulmaceae. *Cedrelospermum* adds to the known diversity of the family and contributes to our understanding of plasticity in characters of fruits and foliage in the Ulmoideae. The extinct *Cedrelospermum* is more abundantly represented in the fossil record, by both fruits and foliage than most of the extant genera; consequently, its chronological distribution can be traced with greater precision. For example, in western North America we can follow it from *C. nervosum*, with leaves of variable shape and marginal character and small fruits to *C. lineatum*, with more constant leaf morphology and larger fruits.

As presently understood from the fossil record of pollen (Muller, 1981) and leaves (Takh-tajan and Zhilin, 1982; Burnham, 1986), the Ulmoideae evolved and diversified during the latest Cretaceous and early Tertiary (Manchester, in press). The oldest records are based on pollen from the Maastrichtian of North and South America and Asia reviewed by Muller (1981). Leaves of Ulmoideae are common at some localities in the Paleocene of North America (Brown, 1962; Hickey, 1977; Burnham, 1986) and have usually been assigned to modern genera. I accept these Paleocene leaves as valid records of the Ulmoideae, but their assignment to modern genera is questionable. Burnham (1986) noted that the Paleocene species attributed to *Zelkova* and *Chaetoptelea* have more variable morphology and lower vein densities than later Tertiary and modern species of these genera. Unequivocal fruits of extant ulmoid genera are conspicuously absent from the Paleocene sediments where these leaves occur although the fruits are commonly found in association with the foliage in Neogene deposits (Manchester, in press).

The earliest appearance of a modern genus of Ulmoideae that can be confirmed by both fruits and foliage is that of *Ulmus* (*Chaetoptelea*) in the early Eocene of western North America (MacGinitie, 1941; Burnham, 1986;

Manchester, in press). Leaves closely resembling those of extant *Zelkova* ("Morphotype C" of Burnham, 1986) appear in the early part of the middle Eocene, and the genus is confirmed in the middle Oligocene by twigs bearing both fruits and leaves from Manosque, France (Saporta, 1891; refigured Manchester, in press).

The appearance of *Cedrelospermum* in the early middle Eocene is long after the initial radiation of Ulmoideae recorded by pollen, and appears to have coincided approximately with the appearance of the first extant genera, i.e., *Ulmus* and *Zelkova*. *Cedrelospermum* may thus be viewed as a product of the same radiation that produced these modern genera, rather than as an ancestral lineage.

An apparent trend of increasing fruit size in *Cedrelospermum* through the Tertiary may have some utility in biostratigraphy both in North America and Europe. Fruit length is a useful criterion for distinguishing the two North American species (Table 1). Although there is some overlap, most of the specimens of *C. nervosum* (middle Eocene) are less than 1 cm in length (\bar{x} = 7.5 mm) whereas most specimens of *C. lineatum* (lower Oligocene) are greater than 1 cm in length (\bar{x} = 11 mm). In Europe the earliest occurrence of *C. aquense* from the late Eocene of Häring (Fig. 45; Ettingshausen, 1885) has the smallest fruits (5 to 7.5 mm, based on 5 specimens at GBV and NHMV). Fruits from the late Oligocene of Rott (Fig. 46, 47) are more variable in size than those of the American populations (Table 1), but average the same length as those of *C. lineatum* (\bar{x} = 11 mm). Fruits from younger localities average still larger; Ruffle (1963) reported that the fruits from the late Miocene of Randecker Maar range from 7 to 17, normally 15 mm long (based on at least 17 specimens). Whether the size differences among European populations are correlated with differences in foliage or other organs and indicative of species differences remains to be determined. The increased overall fruit size is accompanied by increased endocarp size, suggesting that the amount of food reserves was enhanced by this trend.

ECOLOGY—The abundance of isolated *Cedrelospermum* leaves in the Green River and Florissant deposits and the relatively thin texture of the laminae, suggest that *Cedrelospermum* was deciduous. Although young leaves were present at the time of flowering, pollen size and morphology are consistent with the interpretation that *Cedrelospermum* was wind-pollinated as are most or all extant *Ulmaceae*.

This genus may have produced much of the dispersed *Ulmus-Zelkova* type pollen present in the Green River (K. Newman, personal communication, 1988) and Florissant (E. Leopold, p. 362–363 in Penny, 1969) palynofloras.

The relatively small-seeded fruits of *Cedrelospermum*, with wings obviously adapted for wind dispersal, suggest that it was an early successional plant that could establish seedlings quickly in areas of open sunlight. Nearly all localities from which *Cedrelospermum* has been recovered, both in Europe (Mai, personal communication, 1987) and North America, are lacustrine volcanic ash deposits. The distinctive leaves and fruits are conspicuously absent from lignitic and clay deposits. Therefore, the known species of this genus were probably colonizers of areas disturbed by volcanic ash deposition. Among extant *Ulmaceae*, some species of the celtoid genera *Trema* and *Parasponia* occupy a niche similar to that envisaged for *Cedrelospermum*; Soepadmo (1977) states that they "come up in dense seral stands on eruptiva, on fresh volcanic ash . . . and are almost invariably an important constituent of thickets, seral regrowths, and secondary forest . . ."

Although edaphically restricted, *Cedrelospermum* must have had a rather broad climatic tolerance. It is represented in vegetation ranging from tropical or subtropical rain forest (e.g., the Nut Beds deposit of the Clarno Formation; Manchester, 1981) to seasonally dry tropical (e.g., the Green River Formation; Leopold and MacGinitie, 1972) to temperate mixed mesophytic (e.g., the Oligocene Gray Ranch flora Oregon; Brown, 1946).

Cedrelospermum is among the limited number of taxa that span the Eocene-Oligocene boundary in western North America, and thus was not immediately eliminated by the climatic cooling documented near the end of the Eocene (Wolfe, 1978) that resulted in massive range reductions and extinction of numerous broad-leaved evergreen taxa. However, the two American species recognized here correspond, respectively, to the Eocene and Oligocene, and it is possible that their morphological differences may in part be a response to climatic factors. Although abundantly represented at Florissant, the genus had diminished in importance by the early Oligocene in Oregon (very few specimens in the Bridge Creek flora) and is not known from any of the Miocene floras of North America. Despite the apparent Oligocene extirpation of *Cedrelospermum* in North America, the genus continued to survive in Europe even into the middle or late Miocene. Curiously, it does not appear to have colonized

eastern Asia, a region in which many genera of mixed mesophytic ecology survived during the Pleistocene.

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